Vol. XIX. *September, 1910.* *No. 4*

BIOLOGICAL BULLETIN

ACCESSORY CHROMOSOMES IN MAN.

MICHAEL F. GUYER,

UNIVERSITY OF CINCINNATI.

Since the publication of my papers on the spermatogenesis of the guinea and of the chicken respectively (Guyer '09*a*, '09*b*) in which was recorded the finding of a chromosome or chromosome complex comparable to the "odd," "accessory" or "X-element," described so frequently of late as occurring in a wide range of the Arthropoda, particularly the Tracheata, I have examined material from other vertebrates and can at present record its presence in the rat, its probable occurrence in the pigeon (although this will require some further corroboration), and its conspicuous occurrence in man. Inasmuch as the material for its study in the rat is in the hands of a student for further investigation, I shall confine myself in this paper to a description of the two accessory chromosomes as found in man, together with other features of human spermatogenesis.

For my studies on man I have been fortunate in being able to obtain exceptionally good material through the courtesy of my colleague, Dr. Paul. G Woolley. The subject from which the testicular material was secured was a negro thirty years of age who had died suddenly from the rupture of an aortic aneurism (Case no. 156143, Pathological Records, the Cincinnati City Hospital). A testis was removed within between an hour and an hour and a half after death while the body was still warm and slices were placed immediately into Gilson's and into Bouin's fluids.

The mounted sections were from five to twelve microns thick. Most of them were stained in Heidenhain's iron-hæmatoxylin

and counter-stained with Congo red or acid fuchsin, although Delafield's hæmatoxylin was used with some.

An abundance of cell divisions were found to have been in progress at the time of death. In a given field of the microscope, in a favorable region, it was not unusual to observe as high as six or seven cells in various phases of division. As many as five or six of such areas might exist in a single section, although it was more usual to find only one or two. The material was very uneven in that slides would be found in which section after section showed division stages, while in others divisions were scarce. These facts indicate that there were proliferating and resting zones in the testis. The stages found in most abundance were the metaphases and late prophases of the primary spermatocytes. It was a comparatively simple matter to find spindles on which the ordinary chromosomes were in metaphase with the two accessories, closely associated, well removed toward, or at, one pole (Figs. 6, 7, 8 and 9).

In the literature of the subject much confusion prevails regarding the number of chromosomes characteristic of man. There is wide disagreement in the counts of different observers and there seems to have been a great dearth of material showing division stages. Most of the enumerations are based on observations of from two to eighteen cells and these often in questionable stages of preservation. The great difficulty apparently has been to secure material which was sufficiently fresh or which was not diseased tissue that is notoriously irregular as regards karyokinetic phenomena.

As early as 1881 Flemming discussed mitosis in the case of man illustrating it with some six figures (Taf. 3, Figs. 11–16) of which Fig. 16 is from leucocytes of leucemic blood, the others, from the corneal epithelium of two different subjects from each of whom an eye had been removed because of affection of the bulbus. Although at this time he made no definite record of the number of chromosomes, his drawings show them to be considerably in excess of sixteen, the number later announced by Bardeleben ('92).

Writing several years later, however, in response to the 1892 paper of Bardeleben, Flemming ('97), from a reëxamination of

his old material, gives the number of chromosomes as twenty-four. He cites the papers of Hansemann ('91, '93) as the earliest attempts known to him to make a count of the chromosomes of man. But since Hansemann records eighteen in one case, twenty-four in another, and forty in a third, the latter apparently estimated from the spireme stage, and inasmuch as he himself admits that his count was very uncertain, concluding with the statement that, "die Zahl sicher höher als 24 sei," we may fairly disregard it, I think, in the light of modern technique. In this second paper Flemming ('97) states that his count is based on only four cell-divisions in which the chromosomes had just split preparatory to separation. His exact statement of his observations is as follows: "Es gelang das zwar bei keinen ganz sicher, aber bei zweien der vier darin enthaltenen Mitosen doch annähernd; es scheinen in beiden Fällen 24 Doppelchromosomen zu sein. Bei beiden sind es jedenfalls mehr als 22 und, wie ich sagen zu können glaube, weniger als 28; an einiger Stellen decken sie sich so, dasz eine exacte Zählung mir unmöglich wird." Flemming's material had been fixed in one sixth per cent. chromic acid and stained with safranin.

Bardeleben has published three papers ('92, '97, '98) on the spermatogenesis of mammals including man in which he comes to the conclusion that the number of chromosomes in the spermatogonia and spermatocytes of man are sixteen and eight respectively, and in his later papers he sets down four as the number that ultimately reaches the spermatids. That is, there is in successive divisions a reduction in numbers from sixteen to eight and then from eight to four. This is much the condition that I have found prevailing in birds (Guyer, '02, '09).

Wilcox ('00) studied sections from a testis which had been removed from a man fifty-four years old, in an operation for hernia. Although scrotal swelling had existed for a year previous to the operation the testis seemed to be normal in size and appearance. He reports that, "In my material the number seemed to be eighteen, the different counts resulting in figures ranging from fifteen to nineteen." He remarks however upon the striking absence of karyokinetic stages, so that his observations were based upon a very limited number of divisions. Because of

this lack of favorable stages he says: "The whole organ was, therefore, sectioned and in the great number of sections thus obtained, not more than twenty cells were found in mitotic condition."

Wilcox continues: "The few cases of mitosis observed were in spermatocytes of the first order. One could easily distinguish spermatogonia, spermatocytes of the first and second order, spermatids, and numerous nearly mature spermatozoa. The number of the latter to be seen was very large and precludes the assumption that the testis was functionally impaired by age or by hernia. In the opinion of the writer, this condition merely indicates that all the various processes in the spermatogenetic series are not necessarily to be observed as taking place at the same time. I can see no reason why there might not become established in the testis periods of cellular activity alternating with periods of cellular rest."

Unfortunately Wilcox gives no drawings with his paper nor does he state definitely whether he regards the eighteen chromosomes seen in the spermatocytes of the first order as the reduced number or not. He does remark, however, that, "in many cases they were plainly arranged in the tetrad or ring formation which has been observed in a pretty general variety of investigated species," consequently the inference would be that a synapsis had occurred and that one might expect to find in the neighborhood of thirty-six as the somatic number.

The latest investigation on the number of chromosomes in man with which I am acquainted is that of Duesberg ('06). He reviews the work of Hansemann, von Bardeleben, and Flemming and on the strength of his own observations concludes that Flemming's count of twenty-four is correct. The excessive number found by Hansemann he would account for on the basis of the abnormal increase in the number of chromosomes which is likely to occur in pathological tissues. In the case of Bardeleben he is inclined to believe that very thin sections (three microns) are responsible for the smallness of the count since he regards it as probable that part of the cell had been cut away.

The tissue upon which Duesberg worked had been fixed in Flemming's or in Hermann's fluid and stained by the iron-hæ-

matoxylin method. However, the number, twenty-four, which he records for man was not determined by direct count but was inferred from the fact that he found two or three clear cases of twelve chromosomes in the primary spermatocytes. That his finding of twelve in the primary spermatocytes was correct is borne out by my observations but he is not justified, in consequence, in stating that there must be twenty-four in spermatogonial or somatic cell-divisions. My material shows that two of the twelve chromosomes are the univalent accessories, and a clear count of favorable spermatogonial chromosomes reveals only twenty-two. This means in all probability that of the twelve chromosomes of the primary spermatocyte, ten are bivalent and two accessories. Although Duesberg examined the spermatogonial chromosomes he states that he was unable to count them exactly beyond determining that, contrary to the opinion of Von Bardeleben, there were clearly more than sixteen. He states further (p. 477) that, "Je n'ai pas pu les compter exactement, tant à cause de la petitesse des cellules que du nombre assez élevé des chromosomes, mais dans quelques cas favorables où leur numération a pu être entreprise, j'ai obtenu des résultats très voisins de 24, jamais supérieurs à ce nombre dans les cellules normales." And in conclusion he says: "Il résulte de là que le nombre des chromosomes est certainement à mon avis, de 12 dans les spermatocytes et par conséquent de 24 dans les spermatogonies et les cellules somatiques. C'est la confirmation de l'opinion de Flemming."

In the general scheme of the spermatogenesis of man there appears to be nothing unique. One can readily recognize the usual four generations of germ cells; viz., spermatogonia, primary spermatocytes (or spermatocytes of the first order), secondary spermatocytes (or spermatocytes of the second order), and lastly spermatids which transform directly into the spermatozoa. An abundance of easily identified Sertoli or nurse cells are in evidence. Occasional centrosomes were observed in suitably stained preparations but I have not pictured any in my drawings because the preparations from which the latter were made were all so strongly decolorized that the stain had evidently completely disappeared from any centrosomes which might have been present.

The matter of counting the spermatogonial chromosomes, it must be admitted, is one of great difficulty. In the late prophase or equatorial plate stage, the only time at which a count is possible, they lie for the most part in an irregular band around a central clearer area. In the vast majority of cases only a deeply stained mass of small contiguous or overlapping chromosomes is visible in this band and an accurate count is out of the question although one can frequently determine that there are over twenty. In several instances, however, in which the positions of the chromosomes and the degree of the staining were favorable, twenty-two distinct chromosomes, never more, were visible.

There is considerable range in size among the individual chromosomes of the spermatogonia as well as observable differences of form. Most of them were rod-like or oval in shape although some were more nearly spherical. In several though by no means all instances two chromosomes, closely associated, were seen lying at some distance away from the main band, out in the cytoplasm. Taking into account this isolation, the rounded shape of these chromosomes and their relative sizes, it seems very probable that they are the two accessory chromosomes which do not manifest their presence for a certainty until the next division. It will be observed that one is somewhat smaller than the other. This condition obtains also between the two chromatin nucleoli of subsequent stages as well as between the accessory chromosomes whereever they can be identified, and one is led in consequence to strongly suspect that they are all one and the same thing. This inference is all the more justifiable when the relation between the chromatin nucleoli and the accessory chromosomes in some of the lower forms is recalled.

Fig. 2 represents a nucleus of the primary spermatocyte in the spireme stage which shows the two chromatin nucleoli in question. In deeply stained specimens these nucleoli, especially the smaller one, are not always evident but in preparations stained by the iron-hæmatoxylin method and then almost entirely decolorized, even as regards the ordinary chromatin of the spireme they are usually conspicuously visible. It should be mentioned that occasionally other small nucleolus-like granules were observable but since there was no constancy in their presence, size or relationship, I have

felt justified in ignoring them in the present discussion. Fig. 3 represents the spireme in the contraction phase which is not very pronounced in man. It will be observred that the two characteristic chromatin nucleoli still persist.

The primary spermatocytes when ready for division, as has already been stated, reveal twelve chromosomes in late prophase or early metaphase (Figs. 4, 5). In Fig. 4 the two accessories are seen at a glance and the remaining chromosomes, judging from their increased size and changed form, are bivalent, representing the paired univalent chromosomes of the spermatogonium. That is, of the original twenty-two chromosomes twenty have paired to form the ten bivalents of the primary spermatocyte and two have remained unpaired as the accessory chromosomes. In Fig. 4 it is not evident just which two are the accessories although twelve chromosomes are present.

It is obvious from the the figures (Figs. 4–9) that there is considerable difference in the size of the various chromosomes of the primary spermatocyte. Although the attempt was made it was not found possible to always identify the individual chromosomes. They grade down in size from some three or four large ones to two or three small ones but the fluctuations in size, probably due for the most part to differences in the effects of fixation together with different degrees of extraction of the stain, were too great to render identification sure. In very strongly decolorized sections, especially when counterstained with Congo red, one large chromosome in particular frequently exhibited a tetrad-like formation, while the other large ones at times showed more or less definite indications of lobing. In some cases this was sufficiently marked to interfere with accurate counting. In a very few instances, so few I think as to be practically negligible, there appeared to be fourteen instead of the customary twelve chromosomes, but the extra chromosomes always took the form of a tiny pair which I am inclined to think had become split off from one of the ordinary tetrads or which had through some chance never entered into the proper tetrad formation. They were always united by linin-like strands to one or two of the larger chromosomes.

Figs. 6, 7, 8 and 9 show the two accessories in characteristic positions. Side by side, they always pass entire, considerably in advance of the divided ordinary chromosomes, toward one pole.

Of the ordinary daughter chromosomes of this first spermatocytic division, a pair of small elongated ones not infrequently are the first to emerge from the general equatorial mass as shown in Fig. 7. One is led to suspect that they may possibly be comparable to the small pair of chromosomes found so constantly in certain of the Tracheata although the evidence is not sufficiently decisive to make this an established fact.

It is inferred that the division of the primary spermatocyte is the reducing division, not simply because such a division ordinarily occurs at this stage, but from the fact that the chromosomes after divergence (Figs. 10, 11) when compared with corresponding divisions of the secondary spermatocytes are seen to resume more the elongate, rod-like appearance that characterizes the univalent spermatogonial chromosomes, and also because the accessory chromosomes pass over entire to one pole here while they are halved in the next division.

It is evident from the foregoing that as regards chromatin content the result of the division of the primary spermatocyte is the production of two dissimilar cells, one of which receives ten, the other, twelve chromosomes. Fig. 10 is a drawing of one end of a late anaphase of such a division showing twelve chromosomes (10 plus 2 accessory). Fig. 11, in which only ten chromosomes are visible, was drawn from what is probably the reverse end of a somewhat later anaphase than that shown in Fig. 10. It is just possible that it is a prophase of division in a secondary spermatocyte where univalent chromosomes come to the equator, but if so it is the exception rather than the rule, as the secondary spermatocytes ordinarily divide according to a different scheme. In any event the drawing serves to illustrate the fact that some daughter cells of the primary spermatocytes have twelve chromosomes and some only ten.

In places both primary and secondary spermatocytes were found dividing in the same field and one is led to conclude that either there was no intervening period of rest between the two divisions or that it was a very brief one. In other instances, however, undoubted resting stages of secondary spermatocyte nuclei were seen in abundance. Approximately half of them showed, under proper decolorization, two chromatin nucleoli of which one was somewhat smaller than the other.

While at the conclusion of the divisions of the primary spermatocytes ten and twelve chromosomes respectively were delivered to the pairs of daughter cells, nevertheless, when the latter as secondary spermatocytes become ready for division, half of them show five and the remainder seven chromosomes. A second pairing of the ordinary chromosomes has evidently occurred, so that there are five bivalent chromosomes in each type of cell and the additional two accessories in the one type. Fig. 12 is a drawing of two contiguous secondary spermatocytes; the one shows five bivalent chromosomes in late prophase, the other more than five chromosomes in metaphase. These two cells are undoubtedly the two daughter cells of the same primary spermatocyte. Fig. 13 shows one daughter cell containing a group of seven chromosomes and the other a late anaphase of division which shows at one end five chromosomes. The number of chromosomes at the opposite pole of the second cell should of course be five although because of the dense massing it could not be positively determined. Fig. 14 represents a late anaphase of division in a secondary spermatocyte which manifestly had had seven chromosomes in metaphase.

Both accessory chromosomes divide in this second spermatocytic division period so that each resulting spermatid receives seven chromosomes (Fig. 16). Fig. 15 represents an anaphase of division in a secondary spermatocyte showing still at the equator of the spindle a lagging chromatic mass. Such a condition was found in several instances and while I believe it to be the two accessory chromosomes which happened merely to be unfavorably placed for observation, I could not positively identify it as such. From the relative positions of the chromosomes as seen in Fig. 16 one would infer that the two sets of accessories were the last to have passed from the equator to the poles of the spindle. Moreover, such a lagging of the accessory in this division was observed in both the guinea and the chicken (Guyer, '09).

It should be mentioned that occasional division stages were visible which, judging from the smallness of the cell and the size and shape of the chromosomes, looked as if they might be secondary spermatocytes preparing to divide with the univalent type (ten or twelve) of chromosome. It is possible, for instance, that

Fig. 11 represents a prophase of the secondary rather than an anaphase of the primary division although I am inclined to think it is the latter. If such simple divisions do take place, however, they are certainly scarce in the material which I have examined so far.

From the foregoing evidence it is manifest that there are in all two distinct groups of spermatids equal in number; namely, those which have received five and those which have received seven chromosomes. These chromosomes soon lose their visible identity and the spermatids are apparently all alike except for the significant fact that approximately half of them, in such preparations as have been stained by the iron-hæmatoxylin method and then all but entirely decolorized show two chromatin nucleoli. It would seem probable that these nucleoli stand in direct genetic continuity with the two eccentric chromosomes seen in the spermatogonia and the two chromatin nucleoli and the accessory chromosomes of the spermatocytes. Fig. 18 represents two contiguous spermatids, one of which shows no nucleoli, the other, two. Comparison with Fig. 19 shows the relative conditions of size between the nucleoli of the spermatid and those of a primary spermatocyte.

As to the meaning of the second conjugation there seems to be at present no clew. I have commented on it briefly in a former paper ('09*a*, p. 509). It is not peculiar to man for I have observed it also in the pigeon ('02, '03), the guinea ('09*a*) and the rooster ('09*b*). Undoubtedly Bardeleben ('97, '98) still earlier saw the same phenomenon in man, for although my results do not agree numerically with his count of sixteen, eight and four respectively, evidently, from the relative proportions in his counts, he had come upon this second curious numerical reduction.

Assuming that the respective chromosomes are more or less qualitatively differentiated, such a numerical reduction, however, by no means necessarily implies that there has also been a second qualitative reduction. Aside from the improbability of such a reduction, the general appearance of the divided chromosomes would not warrant this interpretation; for instead of the elongated univalent type as seen in the spermatogonia or in anaphases of the divisions of spermatocytes of the first order, the daughter chromosomes here retain the rounded appearance and increased size that

is characteristic of the bivalent types (compare Figs. 1, 10 and 11, 13, 14, 15, 16 and 17). Thus while half of the spermatids receive five, and half seven chromosomes, in terms of univalence the numbers would in all probability be ten and twelve respectively.

Inasmuch as the spermatids transform directly into spermatozoa it follows that there must be be two classes of the latter differing with respect to whether they have or do not have the two accessory chromosomes. Thus the conditions in man appear to be very much the same that Wilson ('09) describes for *Syromastes*, one of the squash-bug family (Coreidæ).

Numerous examples of such dimorphism of the spermatozoa have been recorded in various invertebrates, particularly in insects, arachnids and myriapods, and it has been clearly demonstrated that eggs fertilized by spermatozoa which possess this accessory chromosome or chromosome group (there may be one, two, three or even four separate chromatic bodies, depending upon the species) develop into females, those fertilized by spermatozoa which do not possess it, develop into males. Hence the accessory has come to be regarded by some of our most careful and experienced workers as an actual sex determinant. In any event it is obviously associated with the determination of sex either as cause or effect. In the light of numerous recent researches both on plants and animals the idea has rapidly gained ground that sex arises not as was long believed, as a response of the developing organism to stimuli from without, but that under normal conditions at least, it is automatically determined by some internal physiological mechanism.

Inasmuch as this intricate matter has been repeatedly and exhaustively discussed pro and con during the past ten years, it is unnecessary for me to enter into a review of the subject anew. For the general reader who may not have kept in touch with the current literature of the subject, two excellent critiques are now available in the recent papers of Wilson ('09*a*) and Morgan ('10). In these papers one will also find thoroughgoing discussions of the subtle problem as to whether, assuming that the accessories are sex determinants, the matter of sex determination is to be regarded as a qualitative process effected by some inherent peculiarity of the accessory chromosome, or whether the relation of such a chro-

mosome or group of chromosomes to sex is merely a quantitative one, the female type resulting when a greater amount of active chromatin is present. Extensive bibliographies will be found in the recent papers of Wilson ('05, '06, '09), Payne ('09), Morse ('09) and Morgan ('10).

In conclusion I wish merely to point out that as regards accessory chromosomes, conditions prevail among vertebrates (guinea, chicken, rat, man, etc.) similar to those found among numerous Tracheata (and probably certain other invertebrates) where the accessories are undoubtedly associated in some way with the phenomena of sexuality. In *Syromastes* (Wilson, '09*b*), which seems to parallel most nearly the condition found in man, half of the spermatids were found to possess two more chromosomes than the remainder. It was predicted by Wilson that in consequence the somatic cells of the female of this species would show two more chromosomes than the somatic cells of the male. Later the facts were found to be in exact accord with his prediction, the somatic cells of the female containing twenty-four, of the male twenty-two chromosomes. Similar verifications have been made in other tracheate forms.

In the light of these facts we should expect the somatic cells of man to contain twenty-two, and of woman, twenty-four chromosomes. The tissues of the female have not yet been studied with this in mind. Flemming ('97) records the somatic number of chromosomes, determined from corneal cells, as twenty-four but unfortunately he does not record the sex of the subjects from which the material was obtained. If it were a female his count would bear out the interpretation given above.

Summary.

1. Twenty-two chromosomes differing considerably in size occur in all spermatogonia in which a definite count could be made. In a few instances two, apparently the two accessory chromosomes, were seen considerably to one side of the main mass of chromosomes, surrounded by a small clear court of cytoplasm.

2. Twelve chromosomes appear for division in the primary spermatocyte, of which ten are evidently bivalent and two accessories.

3. The two accessory chromosomes pass undivided to one pole of the spindle considerably in advance of the other chromosomes, with the result that half of the daughter cells in this division receive twelve, and half, only ten univalent chromosomes. This is evidently the reduction division.

4. The ten univalent chromosomes which passed to the one secondary spermatocyte unite again in pairs, at least in the majority of cases, to form five bivalent chromosomes which appear at the equator of the spindle when the cell is ready for division. The division here is presumably an equation and not a second reduction division, judging from the size, shape and general appearance of the resulting daughter chromosomes. Thus while each of the spermatids formed as a result of this division receive only five chomosomes, the latter are bivalent and equivalent to ten of the somatic or spermatogonial chromosomes. There is some slight evidence that the secondary spermatocytes may occasionally divide with these chromosomes in their original condition of univalence.

5. Ten of the twelve chromosomes which passed to the other pole of the spindle in the primary spermatocyte behave in precisely the same way as described in the last paragraph. The two accessory chromosomes come to the equator of the spindle in the secondary spermatocyte with the five bivalents thus making in all seven. Each accessory now divides so that the resulting spermatids each receive seven chromosomes; that is, five bivalent plus two accessory, or the equivalent of twelve univalent chromosomes.

6. In reality, then, of the total number of spermatids, half have in all probability received ten, and half, twelve (10 plus 2) univalent chromosomes. Inasmuch as the spermatids transform directly into spermatozoa, there must be two classes of the latter differing with respect to whether they have or do not have the two accessory chromosomes.

7. It is a significant fact that approximately half the resting spermatids when strongly decolorized after iron-hæmatoxylin staining, show two chromatin nucleoli and half do not. It seems probable that these nucleoli may correspond to the accessory chromosomes and are to be identified with the two

nucleoli of the primary spermatocyte and the two eccentric chromosomes seen in the spermatogonia.

8. It is probable that in man and certain other vertebrates, as in the insects, myriapods and arachnids, the accessory chromosomes are in some way associated with the determination of sex.

LITERATURE.

Bardeleben, K. von

'92 Ueber Spermatogenese bei Säugetieren. Verhandl. Anat. Gesellsch. Wien.

'97 Beiträge zur Histologie des Hodens und zur Spermatogenese beim Menschen. Arch. f. Anat. und Physiol., Anat. Abth., Supplement.

'98 Weitere Beiträge zur Spermatogenese beim Menschen. Jenaische Zeitschr. f. Naturw., XXXI.

Duesberg, J.

'06 Sur le nombre des chromosomes chez l'homme. Anat. Anz., XXVIII.

Flemming, Von W.

'81 Beiträge zur Kenntnis der Zelle, III. Arch. f. mikr. Anat., XX.

'97 Ueber die Chromosomenzahl beim Menschen. Anat. Anz., XIV.

Guyer, M. F.

'02 Hybridism and the Germ-Cell. Univ. of Cincinnati Bull., Ser. II., Vol. II., No. 21.

'03 Spermatogenesis of Normal and of Hybrid Pigeons. Reprint of an earlier ('00) thesis. Univ. of Cincinnati Bul., Ser. II., Vol. III., No. 22.

'09a The Spermatogenesis of the Guinea. Anat. Anz., XXXIV., Nos. 20–21.

'09b The Spermatogenesis of the Domestic Chicken. Anat. Anz., XXXIV., Nos. 22–24.

Hansemann

'91 Ueber pathologische Mitosen. Virchow's Archiv, CXXIII.

'93 Studien über die Specificität, der Altruismus und die Anaplasie der Zelle, etc., p. 64.

Morgan, T. H.

'10 A Biological and Cytological Study of Sex Determination in Phylloxerans and Aphids. Jour. Exp. Zoöl., VII., 2.

Morse, Max

'09 The Nuclear Components of the Sex Cells of Four Species of Cockroaches. Arch. f. Zellforsch., III., 3.

Payne, Fernandus

'09 Some New Types of Chromosome Distribution and their Relation to Sex. Biol. Bull., XVI.

Wilcox, E. V.

'00 Human Spermatogenesis. Anat. Anz., XVII.

Wilson, E. B.

'05 Studies on Chromosomes, I., II. Jour. Exp. Zoöl., II.

'06 Studies, etc., III. Ibid., III.

'09a Recent Researches on the Determination and Heredity of Sex. Science, XXIX., Jan. 8.

'09b Studies on Chromosomes, IV., V. Jour. Exp. Zoöl., VI.

Explanation of Plate I.

All of the drawings were made with the aid of a camera lucida; their magnification is approximately 1,550 diameters. While the chromosomes are represented as accurately as possible, no attempt has been made to show details of the achromatic structures beyond general appearances and relations. In several cases where the chromosomes were not in the same focal plane they have been drawn carefully in the most favorable plane and then corrected as much as possible from second more accurate drawings of such individual chromosomes as were not in focus in the first drawing.

Fig. 1. Late prophase of spermatogonial division showing twenty-two chromosomes. The two chromosomes lying to one side of the main zone of chromosomes are presumably the two accessories.

Fig. 2. Nucleus of primary spermatocyte showing spireme stage with two chromatin nucleoli.

Fig. 3. Nucleus of primary spermatocyte showing the contraction-phase of the nuclear contents, also two persisting nucleoli.

Fig. 4. Late prophase of division in a primary spermatocyte showing twelve chromosomes. The two lying to one side of the main group are the accessories.

Fig. 5. Late prophase of division in a primary spermatocyte showing twelve chromosomes. Here the two accessories are not readily identified.

Figs. 6, 7, 8, 9. Metaphases of divisions in primary spermatocytes showing the two accessories in characteristic positions passing early to the poles. Fig. 7 shows also two precociously diverging daughter chromosomes.

Fig. 10. One end of a late anaphase of division in a primary spermatocyte showing twelve chromosomes (10 plus 2 accessory).

Fig. 11. Probably one end of a late anaphase of division in a primary spermatocyte, showing ten chromosomes, the accessory chromosomes having gone to the opposite pole; possibly a prophase of division in a secondary spermatocyte in which the ten chromosomes have remained univalent.

Fig. 12. Two contiguous secondary spermatocytes of which one shows five bivalent chromosomes in late prophase, the other more than five chromosomes (probably five bivalent plus two accessory) in metaphase. These two cells are evidently the products of a division of a primary spermatocyte in which ten chromosomes passed to one pole and ten plus the two accessories to the other.

Fig. 13. Two contiguous secondary spermatocytes. One, having just divided, shows five chromosomes at one pole; the chromosomes at the other pole are so massed as to preclude counting although there should be five. The other secondary spermatocyte shows seven chromosomes in late prophase.

Fig. 14. Late anaphase of division in a secondary spermatocyte which has received the two accessory chromosomes, showing seven chromosomes in all.

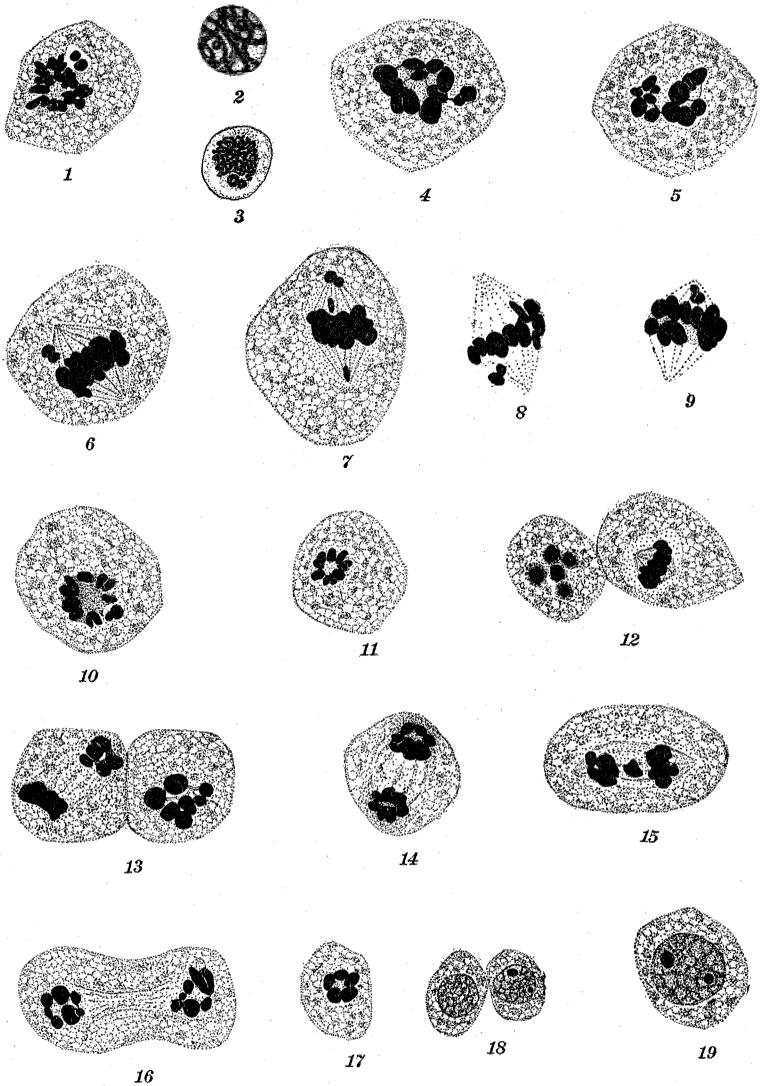
Fig. 15. Anaphase of division in a secondary spermatocyte showing still at the equator a lagging chromatic mass which is probably the two accessory chromosomes although it could not be positively identified as such.

FIG. 16. Late anaphase of division in a secondary spermatocyte which has received the two accessory chromosomes. Each of the latter divides as an independent chromosome at this time.

FIG. 17. One end of a late anaphase of a division in a secondary spermatocyte which had not received the accessory chromosomes.

FIG. 18. Two contiguous spermatids, one without chromatin nucleoli, the other with two. The spermatids in general are about equally divided into these two classes.

FIG. 19. Nucleus of a primary spermatocyte showing two chromatin nucleoli.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19